Ficus microcarpa (Moraceae) naturalized in Southern California, U. S. A.: Linking plant, pollinator, and suitable microhabitats to document the invasion process

RICHARD E. RIEFNER, JR.
Research Associate, Rancho Santa Ana Botanic Garden
1500 North College Avenue
Claremont, California 91711-3157, U.S.A.
rriefner@earthlink.net

ABSTRACT

Ficus microcarpa is native to temperate and tropical Asia, Australasia, and Pacific regions. It is a popular ornamental tree grown in many warm temperate, subtropical, and tropical regions of the world, where it is widely known to escape from cultivation. It is reported here as being naturalized in Los Angeles, Orange, Riverside, San Diego, and Ventura counties, southern California. The invasive spread of *F. microcarpa* follows the introduction of its host-specific pollinating wasp, *Eupristina verticillata*; *E. verticillata* was first reported for California in 1994 from Arcadia, Los Angeles County. The wasp introduction reunited the *F. microcarpa* host plant–*E. verticillata* obligate pollinator mutualism thereby enabling the reproduction and naturalization of both organisms in California. A map showing the current distribution of *F. microcarpa*, citation of voucher specimens, and photographic documentation are provided. Published on-line www.phytologia.org *Phytologia 98(1):42-75 (Jan 5, 2016)*. ISSN 030319430.

KEY WORDS: *Ficus microcarpa*, biological invasions, California, epiphytes, *Eupristina verticillata*, fig wasps, halophytes, invasive plants, mutualisms, ornamental horticulture, urban weeds.

Ficus (Moraceae) is one of the largest and most diverse genera of flowering plants. *Ficus* species occur primarily in subtropical and tropical regions around the world (Berg & Corner 2005). Members of the genus are treated within six subgenera based primarily on their differences in habit and inflorescence morphologies (Berg 2003), and species-specific wasp-dependent pollination syndromes (van Noort & Rasplus 2015). *Ficus* inflorescences are small and borne on the inner walls of a fruit-like and fleshy urn-shaped receptacle, i.e., the syconium, commonly known as a fig (Janzen 1979; Wunderlin 1997). Corner (1997), in a creative portrayal, described the syconium as a "cluster of flowers within a vase." Figs (syconia) are unique enclosed inflorescences that support complex coevolved mutualisms of pollinating and non-pollinating wasp communities (Janzen 1979; Wang et al. 2015). Fig pollination is often regarded as a model for study of coevolution, population genetics, host-parasitoid interactions, community ecology, historical biogeography, and conservation biology (Wieblen 2002).

Ficus microcarpa L.f. (subgenus *Urostigma*, section *Conosycea*) is an evergreen, monoecious tree native from Sri Lanka through India to southern China, Singapore, Taiwan, Japan, the Ryukyu Islands, northern Australia, New Caledonia, and many Pacific Islands, where it grows from sea level to about 1,800 m elevation (Wagner et al. 1999; Berg & Corner 2005; Tan et al. 2009; van Noort & Rasplus 2015; USDA GRIN 2015). *Ficus microcarpa* is a widely planted and popular ornamental tree, even within its native range, that has been introduced to many tropical, subtropical, and warm temperate regions around the world (Dehgan 1998; Rauch & Weissich 2000; Burrows & Burrows 2003; van Noort & Rasplus 2015).

In California, *F. microcarpa* is frequently cultivated along streets in coastal regions because it tolerates salt, wind, drought, and various types of soils, and it is often used for hedges (Brenzel 2007;

Hatch 2007; Perry 2010). *Ficus microcarpa* is extremely hardy, but is sensitive to frost, which restricts its use as an outdoor ornamental (Brenzel 2007; Tan et al. 2009; Perry 2010).

Throughout its range, *F. microcarpa* is known by many common names, including Chinese banyan, Indian laurel, laurel fig, curtain fig, Malay banyan, small-fruited fig, glossy-leaved fig, and many others (Tan et al. 2009; USDA, GRIN 2015; USDA, NRCS 2015). With a long history of use in the horticultural industry and numerous cultivars (Doty & Johnson 1954; Krishen 2006), there has been considerable nomenclatural confusion. The most frequently misapplied names for North American references include *F. nitida* sensu auct. non Thunb., *F. nitida* sensu auct. non L., and *F. retusa* sensu auct. non L. The APC (2015), The Plant List (2015), and Porcher (2015) provide a full synonymy. Confusion in the taxonomic literature began when Ridley (1924) mistakenly referred the Malay banyan to *Ficus retusa* L. (Tan et al. 2009). *Ficus retusa* L. and *F. microcarpa* L.f. are distinct species (Berg 2004; Berg & Corner 2005; The Plant List 2015; van Noort & Rasplus 2015). This misunderstanding persists, particularly among horticulturalists, and many nurseries continue to retail *F. microcarpa* under the old names.

Outside of cultivation, *F. microcarpa* grows on rocks, cliffs and hills, particularly on limestone, along rocky coasts, in beach forests, on floodplains and banks of tidal rivers, along the edge of swamps and mangroves, in rain forests, and frequently as an epiphyte on other trees (Chew 1989; Keng et al. 1990; Corner 1997; Weber 2003; Berg & Corner 2005). In coastal habitats it is often exposed to salt spray and is tolerant of water-logged soils within a wide range of salinity concentrations (Corner 1997; Tan et al. 2009; Yeo & Tan 2011). Accordingly, *F. microcarpa* has been identified as a halophyte (Menzel & Lieth 2003; Yensen 2015). Further, Aronson (1989) characterized it as a hydro-halophyte. In Malaysia, *F. microcarpa* can form monocultures at coastal sites even within its native range (Berg & Corner 2005). *Ficus microcarpa* is also renowned for its adaptability and tolerance to dry, harsh conditions in its native range and where it has been introduced. Throughout its range, it grows in tropical dry forests or dry coastal sites, fragmented and disturbed habitats, summer-dry Mediterranean climates, and frequently in urban environments (Starr et al. 2003; Weber 2003; Anbarashan & Parthasarathy 2013; Uotila 2015).

Ficus species are ecologically significant, keystone organisms because many animals feed upon their figs (Basset et al. 1997; Harrison 2005; Chaudhary et al. 2012). The syconia of *F. microcarpa* are axillary, grow singly or in pairs, measure about 6–10 (12) mm in diameter, and turn pinkish to reddish-green, purplish or black at maturity (Wagner et al. 1999; Berg & Corner 2005; Tan et al. 2009). Its figs are consumed by more than 200 frugivorous vertebrate species, primarily birds, but also bats, rodents, other small mammals, and ants, which act as secondary dispersal agents (Kaufmann et al, 1991; Shanahan et al. 2001; Starr et al. 2003). Pollinated figs of *F. microcarpa* contain small seeds that are easily dispersed and propagate readily in the boughs of host trees, in rock crevices, or on structures like buildings and bridges (McKey 1989; ISSG 2015).

Like most species of the subgenus *Urostigma*, *F. microcarpa* is a strangler fig. The subgenus *Urostigma* consists of about 280 species worldwide and most of them are hemi-epiphytes; i.e., the banyans and stranglers (Rønsted et al. 2008). Banyans produce aerial roots that later become accessory trunks, and the stranglers, which form root baskets around trunks of host trees, begin life as an epiphyte. The strangler fig seeds often germinate about 20–25 m above the forest floor, avoiding competition with ground-dwelling species, thereby increasing survivorship in dense rainforests where little light reaches the ground (Laman 1995; Berg & Corner 2005). Hemi-epiphytes produce aerial, adventitious, or creeping roots that grow down to the ground, which is followed by a transition to an independent or nearly free-standing tree that envelope or gradually kills its host (Berg & Corner 2005). The hemi-epiphyte *Ficus* species utilize host trees for support, but as a result of shading and competition for sunlight, limb breakage, mechanical restriction of trunk growth, and vascular constriction of phloem and xylem tissues caused by the *Ficus*, the host tree often perishes (Putz & Holbrook 1985; Todzia 1986; Kramer 2011).

Many *Ficus* species that are hemi-epiphytes are also lithophytes (Berg & Corner 2005). *Ficus* lithophytes naturally occupy sunny cliff and rock habitats, and in urban environments they readily colonize open niches on buildings and other structures (Jim 1998). In fact, Shuyi (2009) found that many weedy *Ficus* species, which mostly belong to the subgenus *Urostigma*, are hemi-epiphytes and/or lithophytes that frequently inhabit anthropogenic and/or open natural cliff and rock habitats.

Species of *Ficus* exhibit one of the most extreme obligate nursery mutualisms known in nature and represent one of the few cases where active pollination behavior by fig wasps (Family Agaonidae; Hymenoptera) has evolved (Janzen 1979; Herre et al. 1996; Cook & Rasplus 2003; Yang et al. 2013). These wasps possess extreme host specificity and life cycles that are closely synchronized with the host fig's phenology (Wieblen 2002; Cruaud et al. 2010). *Ficus* species, therefore, can only be pollinated by their host-specific agaonid wasp, and in turn, the agaonid wasp can only reproduce if its associated species-specific *Ficus* syconia are present (Janzen 1979; Weiblen 2002; Starr et al. 2003); with some exceptions (Machado et al. 2005). Accordingly, non-native species of *Ficus* that establish in new regions do not produce fertile seed until their species-specific pollinators have also been introduced (Ramirez & Montero 1988).

The Old World fig wasp *Eupristina verticillata* Waterston (Agaonidae) is the pollinator of *F. microcarpa* (Ramirez & Montero 1988; van Noort & Rasplus 2015). Sexual reproduction is possible only if this specific fig wasp pollinator is present (Wang et al. 2015). There are a number of examples that document the transportation between countries and/or continents, and the re-establishment of the *F. microcarpa* host plant–*E. verticillata* obligate pollinator partnership that results in mutual reproduction of the two organisms. Prior to the 1920s–1930s, about the time when *E. verticillata* was purposely introduced to Hawai'i for reforestation, *F. microcarpa* produced neither mature fruit nor fertile seed in Hawai'i, and did not spread beyond cultivation (Pemberton 1939; Stange & Knight 1987; Beardsley 1998). In Florida, *F. microcarpa* was widely planted as an ornamental and a street tree, but began to spread outside cultivation only after *E. verticillata* arrived accidentally, sometime in the 1970s (Kaufman & Kaufman 2012). Apparently, the wasp was an unintentional introduction that may have been transported live in fruit from other infestations (McKey 1989). More recently, *E. verticillata* was unintentionally introduced to southern California where it was discovered in 1994 in Arcadia, Los Angeles County (CDFA 1994; Beardsley 1998). The J.W. Beardsley voucher specimen is housed at the Bernice Pauahi Bishop Museum in Honolulu (BPBM); California: Arcadia, ca. 600 ft., viii.1994, reared ex. fruit of *Ficus microcarpa* L.f. During the last 50 years, *E. verticillata* has also been accidentally or intentionally introduced and established in several other Mediterranean climate and desert regions, including Italy, Madeira, Malta, Canary Islands, Spain, Tunisia, Turkey, and the United Arab Emirates; see Wang et al. (2015) for a global review.

In the continental United States and its territories, *F. microcarpa* is reported growing outside of cultivation in Florida, Hawai'i, and Puerto Rico (Wunderlin 1997; USDA, NRCS 2015). Wunderlin (1997) noted that *F. microcarpa* was observed growing outside of cultivation in the Los Angeles area, southern California, but voucher specimens were not available for examination and it was not included in his treatment. *Ficus microcarpa* was first reported for California by O'Brien (1995) from the Los Angeles Civic Center area, with a second unconfirmed report from Pacific Palisades, also in Los Angles County. Randall (1997) in a CalEPPC Weed Alert cited O'Brien and reported *F. microcarpa* as possibly established or persistent. CNPS (2007) informally noted it growing at Echo Park and escaping elsewhere in downtown Los Angeles. The Consortium of California Herbaria (CCH 2015), however, posts records of ornamental trees persistent in old neighborhoods near El Segundo and on the Palos Verdes Peninsula, Los Angeles County, but no records for naturalized populations in Los Angeles County or elsewhere. Apparently, voucher specimens were never collected and distributed to herbaria to document early observations of the species escaping cultivation.

Ficus microcarpa, therefore, has not been cited for California by The Jepson Manual, Second Edition, or online by The Jepson Flora Project (Whittemore & McClintock 2012; Jepson Flora Project 2015). It has also not been included in other California publications that identify non-native species growing spontaneously outside of cultivation, including Hrusa et al. (2002), DiTomaso and Healy (2003, 2007), Roberts et al. (2004), Rebman and Simpson (2006), Clarke et al. (2007), Grewell et al. (2007), Dean et al. (2008), Roberts (2008), and Prigge and Gibson (2012).

Following the introduction of its host-specific pollinating wasp (*E. verticillata*), *F. microcarpa* has naturalized and is reported here growing spontaneously outside of cultivation in Los Angeles, Orange, Riverside, San Diego, and Ventura counties, southern California, U.S.A. *Ficus microcarpa* is widespread in urban environments where it grows on old masonry and concrete structures such as bridges, freeway underpasses, drainage channels, gutters, and sidewalk curbs. It is also epiphytic on the trunks of landscape trees, primarily palm trees. *Ficus microcarpa* also grows on the bank of an urban tidal channel and along the seashore on a harbor bulkhead within the salt spray zone. In native plant communities, *F. microcarpa* grows rarely in ephemeral calcareous-saline seeps in crevices of cliff and rock outcrops along the immediate coast.

For urban and native plant community sites, the plant appears to germinate from seed dispersed in figs eaten by birds or small mammals, and the seedlings establish and grow without human intervention or intentional summer watering. *Ficus microcarpa* is to be expected elsewhere in similar habitats at other localities wherever conditions for its growth are favorable and wherever its pollinating wasp co-occurs with ornamental plantings or expanding naturalized populations. Discussions about its naturalized habitats, substrate ecology, urban weeds, adaptive field survey protocols, and invasive plant status are provided. A distribution map, citation of voucher specimens, and photographic documentation of occurrences in southern California are also included.

MATERIALS AND METHODS

In October 2008, an approximately 1 m tall shrub was discovered growing in the crevice of a coastal rock outcrop seep in Laguna Beach, southern California. In July 2013, an approximately 1.2 m tall shrub was discovered growing in the crevice of a concrete-grouted stone wall along the seashore, also in Laguna Beach. These small shrubs were tentatively identified as *F. microcarpa*. Therefore, casual surveys were implemented to collect material with syconia and confirm the identification of *F. microcarpa* spreading outside of cultivation in southern California.

In February 2014, a nearly 3 m tall naturalized tree with syconia was discovered at Dana Point in Orange County, and in July, 2014, an approximately 3.5 m tall tree with syconia was documented in San Pedro, Los Angeles County. These two trees enabled confirmation of species identification.

Focused Field Survey Program

Following collection of fertile plants and a review of the literature, a focused survey program was designed and implemented in 2014-2015 to identify the naturalized distribution and determine the invasive status of *F. microcarpa* for southern California. Urban habitats including old masonry, concrete structures, and the trunks of palms and other landscape trees, particularly localities in close proximity to cultivated *F. microcarpa* trees, were the focus of surveys conducted for this study. Specific localities were selected for study, including the City of Arcadia, where its pollinator, *E. verticillata*, was first discovered. Other parts of the Los Angeles metropolitan area, including Echo Park and Pacific Palisades were also visited to verify early reports of juvenile *F. microcarpa* plants. Particular attention was devoted to surveying tidal wetlands and calcareous cliff habitats in native communities during routine travels across coastal southern California.

Wherever *F. microcarpa* was located outside of cultivation, data collection included a physical description of the location, GPS coordinates, notes on plant size, substrate, presence of syconia, and photographic documentation. Herbarium specimens were collected to voucher each population, with the exception of eight sites where plants were observed out of reach on upper palm tree trunks; those sites were photographed for documentation. In addition, soil samples were collected from urban masonry, cliff and rock outcrops, and tidal channel habitats and sent to Wallace Laboratories (El Segundo, California) to determine pH, salinity, and calcium carbonate (lime) content to establish preliminary substrate affinities. Citation of voucher specimens follows.

Vouchers: **U.S.A.: CALIFORNIA: Los Angeles Co.:** City of Los Angeles, Boyle Heights, S of Interstate 10, E side of Interstate 5 on bridge at State St., 34°03'11.5848"N 118°12'48.7050"W, elev. ca. 107 m, 1.2 m tall sapling growing in concrete bridge expansion joint, 23 Nov 2013, *Riefner 13-356* (RSA); City of San Pedro, W side of South Harbor Blvd. at West Santa Cruz St., 33°44'39.9156"N 118°16'47.1114"W, elev. ca. 6 m, 0.8 m tall sapling on palm trunk, 13 Jul 2014, *Riefner 14-243* (CDA, RSA); City of San Pedro, Port of Los Angeles, near Los Angeles Maritime Museum, Sampson Way at West 6th St., 33°44'17.7468"N 118°16' 43.3624"W, elev. ca. 1 m, ca. 3.5 m tall tree w/syconia, growing on bulkhead over breakwater rocks within the salt spray zone, 13 Jul 2014, *Riefner 14-245* (RSA, UC, UCR); City of Long Beach, N of East 2nd St. and W of Marine Stadium Park, Alamitos Bay, near docks on Bay Shore Ave. between Monroe Ave. and East Vista St., 33°45' 37.0260"N 118°07' 30.2406"W, elev. ca. 6 m, several 1-1.5 m tall multi-branched saplings on palm tree trunk, growing with *Nephrolepis cordifolia*, 27 Jul 2014, *Riefner 14-260* (CDA, RSA, UCR); City of Long Beach, Belmont Shores, N side of Ocean Blvd. at Prospect Ave., 33°45' 28.8144"N 118°08' 33.6084"W, elev. ca. 4 m, 2 m tall tree w/syconia on palm trunk, 11 Aug 2014, *Riefner 14-284* (CDA, RSA); City of Long Beach, Belmont Shores, N side of Ocean Blvd. between Quincy Ave. and Park Ave., 33°45' 26.8164"N 118°08'28.4510"W, elev. ca. 4 m, several 3- 8 cm tall seedlings growing in crevices along sidewalks and in gutters and several 1-1.5 m tall saplings on palm trunks, 11 Aug 2014, *Riefner 14-287 & 14-288* (CDA, RSA, UCR); City of Long Beach, Belmont Shores, N and S sides of Ocean Blvd. at Termino Ave., 33°47'17.2320"N 118°16' 54.8944"W, elev. ca. 11 m, 5 cm tall seedling growing in street gutter and sapling < 1 m tall on a palm trunk, 11 Aug 2014, *Riefner 14-292* (CAS); Harbor City, W of 110 Freeway, on Figueroa Pl. ca. 0.3 mi N of Anaheim St., opposite of Harbor Park Golf Course, 33°47'17.2320"N 118°16'54.8944"W, elev. ca. 9 m, two trees w/syconia ca. 4.5 - 5.2 m tall and intermingled saplings growing in joints of rough-grouted concrete wall, 6 Oct 2014, *Riefner 14-369* (CAS, RSA, UCR); Harbor City, W of 110-Freeway, Figueroa Pl. at Lagoon Dr., 33°46'54.5736"N 118°16'51.3297"W, elev. ca. 6 m, 3.5 m tall tree w/syconia growing in joint of rough-grouted concrete wall, 6 Oct 2014, *Riefner 14-371* (RSA, UCR); Harbor City, underpass on West L St. at Figueroa Pl., W side of 110 Freeway, 33°47'09.3876"N 118°16'53.7267"W, elev. ca. 6 m, ca. 1.5 m sprawling tree growing in joint of concrete wall ca. 8 m above ground, 6 Oct 2014, *Riefner 14-373* (RSA, UCR); City of Los Angeles, Westlake, Echo Park, S side of Bellevue Ave. near Glendale Blvd., 34°04'12.9828"N 118°15'39.0865"W, elev. ca. 121 m, 2 m tall saplings growing on upper palm trunk and crown foliage, 18 Apr 2015, *Riefner 15-112 photographic documentation*; City of Los Angeles, Westlake, Echo Park, Echo Park Ave., N of Bellevue Ave. and S of Laguna Ave., 34°04'18.7572"N 118°15'36.2852"W, elev. ca. 122 m, 1 - 2 m tall saplings growing on upper palm trunk and crown foliage, 18 Apr 2015, *Riefner 15-113 photographic documentation*; City of Los Angeles, Westlake, E side of Rampart Blvd. immediately S of West 3rd St., 34°04'02.9892"N 118°16'41.3940"W, elev. ca. 95 m, 1.5 m tall saplings growing on palm trunk among crown foliage, 18 Apr 2015, *Riefner 15-115 photographic documentation*; City of Los Angeles, Westlake, MacArthur Park, W of South Alvarado St. along 7th St., 34°03'24.6708"N 118°16'39.1415"W, elev. ca. 84 m, 1.8 m tall stout saplings growing on palm trunks and crown foliage, 18 Apr 2015, *Riefner 15-118* (RSA, UCR); City of Los Angeles, Lincoln Heights, S side of West Avenue 26 at Interstate 10 bridge, 34°04'59.8512"N 118°13'18.6930"W, elev. ca. 109 m, 1 m tall sapling and 2.2 m tall tree growing in joints of a concrete bridge and freeway retaining wall, 25 Apr 2015, *Riefner 15-127* (RSA); City of Los Angeles, Mt. Washington, W side of North Figueroa St. at Woodside Dr., 34°05'53.4120"N 118°12'19.9891"W, elev. ca. 140 m, 1.2 m tall stout sapling growing in crevice of stone wall, 25 Apr 2015, *Riefner 15-129* (RSA, UCR); City of Santa

Monica, both sides of Ocean Ave., N and S of Santa Monica Blvd., 34°00'47.9880"N 118°29'50.9528"W, elev. ca. 30 m, several 0.5 - 1.2 m tall saplings growing on the trunk and crown of palm trees, 25 Apr 2015, *Riefner 15-132* (RSA); City of Santa Monica, Pacific Palisades, along Sunset Blvd. at Pampas Ricas Blvd./Chautanqua Blvd. intersection, 34°02'27.8268"N 118°31'06.8789"W, elev. ca. 101 m, 1.5 m tall stout sapling growing in the crown of a palm tree, 25 Apr 2015, *Riefner 15-134 photographic documentation*; City of Arcadia. S side of Interstate 210, W of Colorado Blvd. between Second St. and La Porte St., 34°08'42.1728"N 118°01'33.2106"W (approximate data), elev. ca. 153 m, 2.5 m tall tree growing beneath freeway overpass in curb crevice along paved parking lot, 2 May 2015, *Riefner 15-138* (CDA, RSA); City of Glendale, Los Angeles River, Glendale Narrows Riverwalk, Flower St. W of Fairmont Ave., 34°09'23.7960"N 118°17'00.7107"W, elev. ca. 146 m, 1 m tall shrub growing in joint of a concrete retaining wall along river channel, 2 May 2015, *Riefner 15-141* (CDA, RSA); City of Glendale, Los Angeles River, Glendale Narrows Riverwalk, Fairmont Ave. E of Flower St., 34°09'23.1912"N 118°16'53.1647"W, elev. ca. 145 m, 1 m tall shrub growing in joint of concrete retaining wall on river channel at culvert outflow pipe, 2 May 2015, *Riefner 15-143 photographic documentation*; City of Carson, E side of 110 Freeway along 190th St., 33°51'41.9220"N 118°17'04.7618"W, elev. ca. 11 m, two ca. 2 m shrubs growing on the underpass wall and one 2 m tall shrub w/syconia growing in sidewalk/curb crack, E side of the Dominquez Channel, 19 Jul 2015, *Riefner 15-200* (CAS, CDA, RSA, UCR); City of Carson, Dominguez Channel at Figueroa St., S channel bank, 33°51'28.9836"N 118°16'53.7498"W, elev. ca. 7 m, single 2.2 m tall shrub w/syconia growing on channel bank with *Parietaria judaica* adjacent to tidal waters with *Atriplex* and *Salicornia*, 19 Jul 2015, *Riefner 15-203* (CAS, RSA); City of Los Angeles, on 43rd St. bridge, W side of 110 Freeway, E of Flower St., 34°00'19.6992"N 118°16'53.4046"W, elev. ca., 58 m, single ca. 3.2 m tall tree w/syconia growing in concrete expansion joint, 26 Jul 2015, *Riefner 15-207* (CAS, CDA, RSA); City of Los Angeles, E side of Figueroa St. at 45th St., 34°00'09.5940"N 118°16'57.3457"W, elev. ca. 42 m, seedling < 30 cm tall at base of palm tree trunk, 26 Jul 2015, *Riefner 15-209* (CAS, RSA); City of Glendale, E side of Glendale Freeway (Hwy. 2), Ripple St. at Rosanna St., 34°06'18.5544"N 118°14'57.7060"W, elev. ca. 116 m, two 2 m tall shrubs w/syconia growing in concrete expansion joints on bridge overpass, 26 Jul 2015, *Riefner 15-211* (CAS, RSA, UC); City of Alhambra, N side of 110 Freeway on E side of Garfield St., 34°04'19.6536"N 118°07'21.8492"W, elev. ca. 129 m, single 1.5 m tall shrub growing in concrete expansion joint of bridge overpass, 2 Aug 2015, *Riefner 15-214* (CAS, RSA, UCR); City of Los Angeles, E side of North Mission Rd. between 101 Freeway and Caesar E. Chavez Ave., 34°03'13.8924"N 118°13'34.2949"W, elev. ca. 101 m, 2 Aug 2015, *Riefner 15-216* (CAS, CDA, RSA); City of Malibu, N side of Pacific Coast Highway, E ca. 0.25 mi from Coastline Dr., 34°02'31.0056"N 118°34'07.8423"W, elev. ca. 15 m, single 1.4 m tall shrub growing in crevice of concrete retaining wall, 15 Aug 2015, *Riefner 15-222* (CAS, RSA); City of Santa Monica, Pacific Palisades, N side of Pacific Coast Highway at Sunset Blvd., 34°02'20.0328"N 118°33'14.3335"W, elev. ca. 12 m, sapling on upper palm tree trunk, 15 Aug 2015, *Riefner 15-224 photographic documentation*; City of Covina, N of 10 Freeway, E side of Grande Ave. at Walnut Creek, general vicinity of Fairway Ln., 34°04'30.0540"N 117°52'20.6194"W, elev. ca. 150 m, 1.3 m tall shrub and seedling growing in joints of concrete drainage channel, 21 Aug 2015, *Riefner 15-341* (CAS, RSA, UCR); City of Los Angeles, Universal City, W side of Barham Blvd. immediately S of DeWitt Dr., 34°07'53.4540"N 118°20'41.4011"W, elev. ca. 238 m, 8 dm tall sapling on palm trunk at base of tree, 23 Aug 2015, *Riefner 15-346* (CDA, RSA); City of Los Angeles, Toluca Terrace, E side of Cahuenga Blvd., S ca. 0.2 mi from Magnolia Blvd., 34°09'59.6232"N 118°21'41.9063"W, elev. ca. 188 m, 2 dm tall seedling at base of cinder block wall along sidewalk, 23 Aug 2015, *Riefner 15-348* (CAS, RSA).

Orange Co.: City of Laguna Beach, vicinity of West St. and Pacific Coast Hwy., 33°30'17.5176"N 117°44' 52.3291"W, elev. ca. 8 m, 1 m tall shrub in seep on coastal bluff outcrop, 22 Oct 2008, *Riefner 08-312* (CAS, RSA), same locality, 3 Jun 2014, *Riefner 14-149* (RSA); City of Laguna Beach, Heisler Park near Recreation Point, SW of Cliff Dr. at Myrtle St., 33°32' 38.1084"N 117°47'34.1096"W, elev. ca. 7 m, stout shrub 1.2 m tall growing in crevice of concrete-grouted stone wall, 11 Jul 2013, *Riefner 13-139* (CDA, RSA); City of Dana Point, W ca. 0.1 mi from Island Way along Dana Point Harbor Dr., cliff immediately S of Santa Clara Ave. and Amber Lantern St., 33°27'48.3192"N 117°42'05.4726"W, elev. ca. 11 m, ca. 3 m tall tree w/syconia growing in sandstone cliff crevice, 24 Feb 2014, *Riefner 14-66* (CAS, RSA, UC, UCR); City of

Newport Beach, N side of Pacific Coast Highway at Riverside Ave., 33°37'13.4472"N 117°55'26.8840"W, ca. 6 m, seedlings in gutter and joint of concrete street drain, 14 Jun 2014, *Riefner 14-169* (CAS, RSA); City of Laguna Beach, N side of North Coast Highway near intersection with Cliff Dr., 33°32'37.1580"N 117°47'15.1785"W, elev. ca. 10 m, saplings growing in crevices of concrete-grouted stone wall, 21 Jun 2014, *Riefner 14-186* (CAS, CDA, RSA); City of Irvine, S side of Red Hill Ave. bridge E of 405 Freeway north-bound lane, 33°41'14.6004"N 117°51'59.0304"W, elev. ca. 31 m, 2 m tall tree growing in concrete bridge expansion joint, 6 Jul 2014, *Riefner 14-222* (CAS, RSA); City of Seal Beach, N side of Westminster Blvd. ca. 0.1 mi W of Road B, 33°45'35.0784"N 118°05'05.4978"W, elev. ca. 3 m, ca. 1.2 m tall sapling growing in joint of concrete drainage channel, 13 Jul 2014, *Riefner 14-241* (CDA, RSA, UCR); City of Laguna Beach, E side of South Coast Highway near Diamond St., 33°31'40.4076"N 117°46'12.2079"W, elev. ca. 25 m, two stout saplings in crevices of concrete-grouted brick wall, 8 Aug 2014, *Riefner 14-273* (CAS, CDA, RSA); City of Irvine, W of Irvine Blvd. and S of Pusan Way, former MCAS El Toro facility, 33°40'42.9456"N 117°42' 56.1746"W, elev. ca. 138 m, scattered seedlings and saplings on palm trunks, growing with *F. rubiginosa*, 26 Nov 2014, *Riefner 14-399* (CDA, RSA); City of San Clemente, San Clemente Municipal Golf Course, Ave. San Luis Rey at Ave. Santa Inez, 33°24'20.1672"N 117°35'43.8156"W, elev. ca. 51 m, 1.8 m tall sapling growing on trunk of cultivated pine tree, 5 May 2015, *Riefner 15-149* (CDA, RSA, UCR); City of San Clemente, Ave. Santa Inez at El Camino Real, 33°24'16.8948"N 117°35'48.8648"W, elev. ca. 44 m, sapling on upper palm trunk, 5 May 2015, *Riefner 15-150 photographic documentation*; City of Costa Mesa, Anton Blvd. on ramp to 405 Freeway, ca. 0.3 mi from intersection of Bristol St. at Sunflower Ave., 33°41'17.6532"N 117°52'26.7539"W, elev. ca. 11 m, 2.5 m tall shrub w/syconia growing in expansion joint of concrete bridge, 18 Jul 2015, *Riefner 15-198* (CAS, RSA, UCR); City of Laguna Beach, S side of Beach St. and E of Broadway Ave. (Hwy. 133), 33°32'38.8428"N 117°47'00.8467"W, elev. ca. 7 m, 15 cm seedling growing at the base of a cinder block wall, growing with *F. rubiginosa*, 27 Aug 2015, *Riefner 15-355* (CAS, RSA); City of Newport Beach, Corona del Mar, on Marguerite Ave. between Fifth Ave. and Fourth Ave., 33°35'57.9012"N 117°52'03.7748"W, elev. ca. 41 m, broad-based tree (ca. 28 cm wide at base), ca. 3 m tall w/syconia growing on palm tree trunk at base of tree, and seedlings and saplings widespread on upper palm tree trunks on the same street, 27 Aug 2015, *Riefner 15-359* (CAS, UC, UCR); City of Newport Beach, Corona del Mar, along Marguerite Ave. S of Fourth Ave., 33°35'55.5468"N 117°52'06.0792"W, elev. ca. 41 m, 1 m tall shrub growing on palm tree trunk at base of tree, 27 Aug 2015, *Riefner 15-360* (CAS, RSA); City of Newport Beach, Corona del Mar, along Marguerite Ave. near Seaview Ave., 33°35'42.8244"N 117°52'19.2982"W, elev. ca. 30 m, 8 cm seedling growing on palm tree trunk at base of tree, scattered saplings on upper palm trunks, growing with *F. rubiginosa*, on the same street, 27 Aug 2015, *Riefner 15-366* (CAS, RSA); City of Rancho Santa Margarita, Trabuco Marketplace, Rancho Santa Margarita Blvd. at Plano Trabuco, 33°38'53.6028"N 117°34'36.3579"W, elev. ca. 363 m, seedling on palm trunk at base of tree, shrubs on upper palm trunks, growing with *F. carica* and *F. rubiginosa*, 29 Aug 2015, *Riefner 15-368* (CAS, CDA, RSA); City of Lake Forest, N side of Interstate 5 Freeway on E side of Lake Forest Dr. bridge, 33°37'42.4848"N 117°43'12.3416"W, elev. ca. 144 m, 1 m tall sapling growing in concrete expansion joint, 29 Aug 2015, *Riefner 15-372* (RSA); City of Anaheim, E side of Lemon St. at East Adele St., 33°50'18.7152"N 117°55'00.8405"W, elev. ca. 48 m, seedlings on palm tree trunk at base of tree and sapling on upper palm trunk, 30 Aug 2015, *Riefner 15-374* (RSA); City of Anaheim, Pearson Park, near center of park, N of North Helena St. and West Cypress St., 33°50'16.7316"N 117°55'05.3326"W, elev. ca. 45 m, 1 m tall shrubs on old masonry around rain gutter, and seedling on trunk of *Schinus terebinthifolius* at base of tree, 30 Aug 2015, *Riefner 15-376 & Riefner 15-377* (RSA); City of Anaheim, Pearson Park, SE section of park, N of North Helena St. and West Cypress St., near intersection of North Lemon St. and West Cypress St., 33°50'15.2664"N 117°55'01.4651"W, seedlings on the trunk of palm trees, *Dracaena draco*, *Olea europaea*, and *Pinus halepensis*, and on calcareous memorial stone, 30 Aug 2015, elev. ca. 44 m, *Riefner 15-379*, *Riefner 15-380*, *Riefner 15-381* (CAS), *Riefner 15-382* & *Riefner 15-383* (RSA).

Riverside Co.: City of Corona, Corona City Park, E side of Rimpau Ave. on N side of Sixth St., 33°52'29.2224"N 117°33'10.1202"W, elev. ca. 211 m, 0.5 m sapling on palm trunk, 8 Aug 2015, *Riefner 15-217* (CDA, UCR); City of Corona, S side of 91 Freeway ca. 120 ft W of Lincoln St., N side of Corona del Rey Apartments, 33°52'53.8176"N 117°34'59.9012"W, elev. ca. 210 m, 1.5 m tall shrub growing from crevice of cinder block wall, 8 Aug 2015, *Riefner 15-220* (CAS, CDA, UC, UCR).

San Diego Co.: City of La Jolla, E side of La Jolla Blvd. near Playa Del Norte St., 32°49'47.7732"N 117°16'36.5555"W, elev. ca. 24 m, 1.5 m stout shrub on palm trunk, 8 Aug 2014, *Riefner 14-271* (CDA, RSA); City of Encinitas, E side of 3rd St. between West G St. and West F St., 33°02'33.5436"N 117°17'42.9849"W, elev. ca. 22 m, seedling on palm trunk, growing with *F. rubiginosa*, 12 Oct 2014, *Riefner 14-377* (RSA, UCR); City of Encinitas, near intersection of Sylvia St. and La Veta Ave., 33°03'04.4712"N 117°17'50.9157"W, elev. ca. 17 m, ca. 3 m tall tree on palm trunk, growing with *F. rubiginosa*, 12 Oct 2014, *Riefner 14-380* (CAS, CDA, RSA, UCR); City of Carlsbad, Harding St. at Camellia Pl., 33°09'18.9504"N 117°20'21.4246"W, elev. ca. 30 m, ca. 2.5 m tall tree w/syconia on upper palm trunk, 30 Apr 2015, *Riefner 15-135 photographic documentation*; City of Carlsbad, along Adams St. near Larkspur Ln., 33°09'17.0424"N 117°20'06.0912"W, elev. ca. 26 m, seedling and 1.5 m tall shrub on palm trunks, 3 May 2015, *Riefner 15-144* (CDA, RSA, UCR); City of Carlsbad, along Adams St. near Magnolia St., 33°09'19.9260"N 117°20'08.3799"W, elev. ca. 27 m, seedling and 0.5 m tall sapling on palm trunks, 3 May 2015, *Riefner 15-147* (CAS, RSA); N of Oceanside, Camp Pendleton, S side of 16th St. ca. 0.1 mi W of Vandegrift Blvd., 33°18'44.5752"N 117°18'43.5613"W, elev. ca. 101 m, 1 m tall shrub rooted in concrete storm drain, 17 May 2015, *Riefner 15-154* (CAS, RSA, UC); City of Oceanside, E side of Carmelo Dr. near Harbor Dr., N of Goodland Dr., 33°12'29.8908"N 117°23'17.4163"W, elev. ca. 23 m, shrub < 1 m tall w/syconia and seedling on base of palm tree trunks, 17 May 2015, *Riefner 15-157* (CDA, RSA, UCR); City of San Marcos, Las Posas Rd. on N side of Highway 78, 33°08'39.6240"N 117°11'28.2435"W, elev. ca. 177 m, shrub < 1 m tall, on concrete bridge in expansion joint, 29 Jun 2015, *Riefner 15-178* (RSA, UCR).

Ventura Co.: City of Oxnard, E side of Oxnard Blvd. (Hwy. 1), S ca. 0.2 mi from West Wooley Rd., 34°11'18.2364"N 119°10'31.9567"W, elev. ca. 9 m, 5 dm tall seedling on palm trunk at base of tree, 16 Aug 2015, *Riefner 15-229* (CAS, RSA).

RESULTS

This study documented 66 populations of *F. microcarpa* naturalized in Los Angeles, Orange, Riverside, San Diego, and Ventura counties, southern California, which are depicted in Fig. 1. Of the documented sites, *F. microcarpa* is reported for the first time for Orange, Riverside, San Diego, and Ventura counties.

In southern California, naturalized *F. microcarpa* plants observed during field surveys range in size from seedlings < 10 cm tall, and saplings, shrubs or small trees growing to over 5 m tall. The six largest trees all bearing syconia were documented from urban and native habitats, including localities in Los Angeles County at Harbor City (Fig. 2), San Pedro (Fig. 3), and the City of Los Angeles (Fig. 4), at Newport Beach (Fig. 5) and Dana Point in Orange County (Fig. 6), and in San Diego County at Encinitas (Fig. 7). Many of the naturalized shrubs and trees in southern California produce figs, and most fertile plants are generally > 2.5 m tall. The smallest fig-bearing plant was a < 1 m tall shrub documented in Oceanside, San Diego County (Fig. 8).

The distribution of the largest trees and shrubs observed during this study is depicted in Fig. 1. The frequency of occurrence suggests that *E. verticillata* was first introduced (likely unintentionally) to southern California in the greater Los Angeles metropolitan area, i.e., first collected in 1994 from Arcadia (Fig. 1). However, the initial introduction may have occurred at a more coastal site, perhaps a port-of-call or the Los Angeles International Airport. O'Brien (1995) speculated that fig wasps may have arrived in the Los Angeles area in 1992, but an earlier date of introduction, perhaps in the 1980s, cannot be ruled out; neither can multiple points or sources of introduction.

Naturalized *F. microcarpa* juvenile plants and small shrubs were found, often unexpectedly, at several inland urban localities, such as Rancho Santa Margarita in Orange County, and Corona in western Riverside County. Based on these observations and the distribution of populations depicted in Fig. 1, *F.*

microcarpa is in the process of a rapid range expansion in southern California.

Southern California Naturalized Populations

Ficus microcarpa thrives outside its natural range wherever its pollinating fig wasp, suitable climate, substrates, and seed-dispersing animals are present. It is often prolific in urban environments (Corlett 2006; Shuyi 2009). In coastal southern California, *F. microcarpa* has established easily in the joints of old masonry, stone and brick walls (Fig. 9), and on concrete structures such as bridges, retaining walls (see Figs. 2 & 4), freeway underpasses, drainage channels, gutters, curbs and sidewalks. It is also epiphytic on the trunks of landscape trees, particularly on palm tree trunks at coastal and inland sites (Fig. 10), primarily *Phoenix canariensis* Chabaud (Arecaceae), but also on *Washingtonia filifera* (André) de Bary, *W. robusta* H. Wendl., and *Butia capitata* (Mart.) Becc. (Arecaceae). *Ficus microcarpa* is also epiphytic on the trunks of *Dracaena draco* (L.) L. (Asparagaceae), *Olea europaea* L. (Oleaceae), *Pinus halepensis* Miller, *P. pinea* L. (Pinaceae), and *Schinus terebinthifolius* Raddi (Anacardiaceae); taxonomy follows Baldwin et al. (2012) or FNA (2015). It also grows on an old wood post, and a bulkhead along harbor shores within the salt spray zone (see Fig. 3). *Ficus microcarpa* has also been found on the bank of an urban tidal channel, Dominguez Channel (Fig. 11). In native plant communities in southern California it has been found rarely on calcareous-saline cliff (see Fig. 6) and rock outcrops (Fig. 12) along the immediate coast.

Based on a preliminary sampling, laboratory analyses using saturation extracts of soils taken within the root zone along tidal shoreline habitat and cliff/rock outcrop crevices indicate the substrates are slightly to moderately alkaline (7.02–8.31 pH), slightly to highly calcareous (calcium carbonate), and range from very slightly saline to strongly saline (2.70–>16 dS/m^{-1}). The urban masonry substrate of *F. microcarpa* is moderately alkaline (8.06 pH), highly calcareous, and non-saline (1.01 dS/m^{-1}), which are the expected parameters for cement/concrete substrates (Wikipedia 2015).

At the cited localities, *F. microcarpa* appears to germinate from seed dispersed in figs eaten by birds or small mammals, which establish and grow spontaneously without the aid of human intervention and without intentional summer watering. At some urban sites, however, aerosol drift from irrigation and runoff from hard surfaces may be influential. At numerous coastal and inland sites in southern California, *F. microcarpa* grows on the upper trunks of palm trees well beyond the possible influence of urban waters. For these populations (Fig. 13), mist and ocean fogs, and the inland extent of the summer marine layer may likely provide the moisture needed for seedling establishment and persistence of *F. microcarpa* hemi-epiphytes in arid southern California.

The Urban Epiphyte Flora

Metropolitan areas are particularly vulnerable to non-native species introductions, which can serve as entry pathways for invasions from the urban environment to native ecosystems (van Ham 2013). Often overlooked in southern California, documentation of ornamental plants escaping in urban habitats can provide important information to track the early dispersal and naturalization of these plants in natural areas. *Nephrolepis cordifolia* (L.) C. Presl (Nephrolepidaceae), which grows outside of cultivation on concrete walls, trunks of palm trees, and calcareous cliffs and bluffs in southern California, is an excellent example (Riefner & Smith 2015). Interestingly, Brusati et al. (2014) listed 186 species of ornamentals of greatest concern for introduction and/or invasiveness in California through the horticultural pathway, including *N. cordifolia*, but not *F. microcarpa*. In southern California, *F. microcarpa* co-occurs with *N. cordifolia* at several locations, including native habitats on calcareous cliffs, and it is also epiphytic on the trunks of palm trees in urban landscapes (Fig. 14).

In southern California, it is not unusual to find several species of *Ficus* epiphytic on the same palm tree or along the same street in urban areas, including *F. carica* L. and *F. rubiginosa* Desf. ex Vent. (see Fig.

7), and numerous other plant species that have not been inventoried. Brandes (2007) provides an extensive list of non-native epiphytes growing spontaneously on *P. canariensis* in Mediterranean climate regions. Birds presumably act as the primary vector of dispersal, but wind may also spread spores and other propagules tree-to-tree or from cultivated and naturalized sources. The dispersal of non-native epiphytes on palm trees across urban southern California increases the opportunity for potentially invasive species to naturalize in suitable native habitats. Accordingly, the urban epiphyte flora of southern California requires further study and documentation.

DISCUSSION

Many non-native plants that have naturalized in floras worldwide have been the product of deliberate introductions (Reichard & White 2001; Mack & Erneberg 2002). In addition, many invasive plants are often of horticultural origin (Bell et al. 2003). In fact, more than 60% of the most invasive plants in California were purposefully cultivated (Bossard et al. 2000). Numerous studies also indicate that many species of cultivated *Ficus* naturalize, and often become weedy or invasive (Ramírez & Montero 1988; Nadel et al. 1992; Gardner & Early 1996; Shuyi 2009).

Setting the Stage for Naturalization and the Invasion Process

Once the *F. microcarpa–E. verticillata* mutualism was reunited, three major factors discussed below paved the way for the *F. microcarpa* invasion. First a suitable climate and abundance of cultivated *F. microcarpa* trees in the Los Angeles Basin facilitated the establishment and spread of its host-specific pollinator, *E. verticillata.* Establishment of the pollinator enabled production of fertile fruits that could be dispersed facilitating establishment of *F. microcarpa* outside of cultivation without direct human help. An abundance of fruit-eating birds in the urban forest was available to facilitate seed dispersal. In addition to urban structures, an abundance of palm trees having persistent (marcescent) leaf bases that trap and accumulate organic matter and moisture were present to provide abundant microhabitat establishment sites.

Eupristina verticillata, Pollinator of *Ficus microcarpa*

For the obligate *F. microcarpa–E. verticillata* mutualism, fig wasp abundance is dependent upon the host tree resource (Yang et al. 2013). *Eupristina verticillata* was first discovered near Arcadia, Los Angeles County, California.

The urban forest of the greater Los Angeles metropolitan area provides abundant host tree resources to facilitate the establishment and dispersal of *E. verticillata* in southern California. In the City of Los Angeles, approximately six million trees have been inventoried for the metropolitan area, including 182,170 *F. microcarpa* trees, which comprise 3% of the urban forest; *Cupressus sempervirens* L. is the most frequently planted at 457,180 trees or 7.6% of the urban forest (Nowak et al. 2001). The City of Santa Monica supports approximately 33,800 public trees, of which *F. microcarpa* is the second most frequently planted at 3,088 trees that comprise 9.1% of the urban tree resources (CSM 2015); noteworthy since early unconfirmed sightings of juvenile plants at Pacific Palisades were reported by O'Brien (1995).

Yang et al. (2013) examined the population dynamics of *E. verticillata* and the phenology of a seasonal-fruited 29-tree population of *F. microcarpa* located in Taipei, Taiwan. Their results revealed three seasons of annual fig production correlated with temperature; spring crop, summer-fall crop, and winter trough (low point) seasons. The *E. verticillata* population size showed an increasing trend in spring, reached maximum abundance in summer, and then declined drastically in winter, which is consistent with the seasonal pattern of fig production. Despite the small number of local *E. verticillata* surviving on winter syconia, the *E. verticillata* population for this 29-tree urban stand can increase quickly from nearly zero to over 40,000 wasps within a season when the small number of wasps overwintering on *F. microcarpa* syconia is combined with potentially immigrating wasps from other *Ficus* populations. Thus, this phenological seasonal pattern of fig production, coupled with the fast recovery rate of an *E. verticillata* pollinator population, may explain the worldwide adaptation and invasion of *F. microcarpa* (Yang et al. 2013).

Thereby, the warm-temperate Mediterranean climate of southern California coupled with abundant *F. microcarpa* cultivated host tree resources facilitated the initial establishment and apparently rapid spread of *E. verticillata* following its initial discovery in 1994. During this phase of dispersal, *E. verticillata* likely had few parasitoid fig wasp competitors resulting in an abundance of *F. microcarpa* fertile seed production; see Wang et al. (2015) for further discussion.

***Ficus microcarpa*, the Urban Environment Connection**

In many native habitats numerous frugivores, particularly birds, disperse *Ficus* seeds that germinate in the crevices of trees or rock outcrops (Basset et al. 1997; Shanahan et al., 2001; Harrison 2005; Chaudhary et al. 2012), but a similar scenario plays out in urban environments. *Ficus* seedlings are often conspicuous on structures and the trunks of landscape trees in cities, largely because many urban-dwelling birds consume and disperse fig seeds (Weber 2003; Corlett 2006; Tan et al. 2009). In Florida, Caughlin et al. (2012) also found that fig-eating birds are common in urban areas, which result in high rates of seed dispersal and establishment of *F. microcarpa* juvenile plants in city landscapes. In Hong Kong, *F. microcarpa* comprises 50% of the trees growing spontaneously on stone walls (Jim 1998). Accordingly, *Ficus* species are keystone resources in many urban environments (Lok et al. 2013).

Ficus microcarpa is frequently cultivated, its seed readily dispersed by urban animal vectors, and it is a naturally-occurring lithophyte that favors lime-rich alkaline substrates (Shuyi 2009; Tan et al. 2010; Jim & Chen 2011). *Ficus microcarpa* is therefore a notorious invader of old masonry and grows easily on buildings, bridges, and many other urban structures within its native and introduced range (Jim & Chen 2011). It also tolerates disturbance, nutrient-poor microhabitats, pollution, drought, and is highly adaptable to urban environments (Wen et al. 2004; Li et al. 2005; Shuyi 2009).

In urban southern California, many birds utilize ornamental landscape trees for nesting or roosting (Garrett 1997, 1998; Crooks et al. 2004). As part of the urban scenario, these birds continually defecate fig seeds consumed from cultivated trees, and *F. microcarpa* juvenile plants often establish nearby on structures or the trunks of palm trees.

Palm Tree Susceptibility to Strangler Fig Invasions

Plant morphological features such as epidermal texture and roughness play an important role in epiphyte recruitment (Compton & Musgrave 1993; Male & Roberts 2005). Bark stability and chemistry, water-holding capacity, tree architecture, and other variables can influence epiphyte performance (Wagner et al. 2015).

For the monocotyledons, particularly the palm family (Arecaceae), the presence of marcescent leaf bases (withering but not falling off) or if leaf bases are senescent with the fronds are important for epiphyte establishment. Recruitment of strangler figs on palms in urban Queensland, Australia, is frequently associated, but not always, with leaf base retention; conversely, palm tree species that cleanly sheath (abscission) old leaf bases generally preclude hemi-epiphyte *Ficus* invasion (McPherson 1999). Marcescent leaf bases promote the accumulation of detritus, thereby providing important microhabitats for hemi-epiphyte *Ficus* seed retention, germination, and seedling establishment (Kramer 2011). The detritus trapped behind persistent leaf bases is often higher in organic matter, nitrogen, magnesium, and potassium than soils located on the ground at the base of the palm tree (Putz & Holbrook 1989). In South Florida, Kramer (2011) concluded palm species with marcescent leaf bases, i.e., the *Sabal* palms and *P. canariensis* were the most susceptible to *Ficus* hemi-epiphyte invasions. In addition, Aguirre et al. (2009) found the abundance and species richness of epiphytes was higher on palms than on non-palm tree substrates, and that *Ficus* hemi-epiphytes are strongly biased toward palm tree hosts.

In Mediterranean ecosystems, Brandes (2007) found that *P. canariensis* provides a specialized substrate for epiphyte recruitment, including *F. carica* and *F. microcarpa*. *Phoenix canariensis* is a popular landscape tree in warm climates throughout the world, and it is extensively planted in southern California (McMinn & Maino 1981; McPherson et al. 2001; Zona 2008; Trent & Seymour 2010), which likely aided the establishment and dispersal of *F. microcarpa* in southern California.

In addition to *P. canariensis*, the fan palms (*W. filifera*, *W. robusta*) are extensively cultivated along streets and parks in California (McMinn & Maino 1981). They are prized for their ease of culture, fast growth, and handsome ornamental form, and both palms are frequently planted together in urban landscapes (Hodel 2014). *Washingtonia robusta*, in particular, is one of the most common ornamental trees cultivated in southern California (McPherson et al. 2001; Nowak et al. 2010; CSM 2015). Although *Washingtonia* species have persistent leaf bases, the dead fronds persist and form a 'skirt' (Simono 2012). In a study of tree ferns, Brownsey and Page (1986) found the retention of dead fronds form a fringing skirt that deters establishment of epiphytes and climbing vines. In southern California, however, routine maintenance activities trim dead fan palm skirts of urban landscape trees thereby exposing the leaf-base niche and rough bark textures that provide favorable microhabitats for *Ficus* hemi-epiphyte recruitment.

Despite the humid environment of subtropical and tropical rainforests, hemi-epiphytes can be subjected to extremes of moisture availability, including drought-like conditions associated with the epiphytic habitat (DeNiro et al. 1985; Putz & Holbrook 1989). Accordingly, strangler figs have evolved special morphological and physiological adaptations to deal with the resource limitations imposed by the epiphytic environment, including waxy leaves with sunken stomata and fleshy stem tubers that alleviate water stress (Schmidt & Tracey 2006).

Given the nature of *Ficus* seed dissemination by urban birds, high propagule pressure associated with widespread cultivation, and adaptations of the strangler figs to alleviate water stress, it is not surprising to find *F. microcapra* utilizing *P. canariensis* and other palm tree substrates as a stepping stone for dispersal across southern California's urban environment.

Invasive Plant Status

In the Global Compendium of Weeds, *F. microcarpa* is listed as a weed, sleeper weed, agricultural weed, noxious weed, introduced species, garden escape, environmental weed (invasive, or species that invades native ecosystems), naturalized or a cultivation escape (Randall 2002; HEAR 2015). *Ficus microcarpa* is reportedly potentially invasive, weedy, or of environmental concern where its specialist pollinating wasp has also been introduced (Randall 2012; HEAR 2015).

Ficus microcarpa has been documented as an invasive species in the New World for Bermuda, Florida, Hawai'i, and Central and South America (Ramirez & Montero 1988; McKey 1989; Nadel et al. 1992; Weber 2003; Caughlin et al. 2012; Wang 2014; GB 2015; HEAR 2015; ISSG 2015). It is classified as an environmental weed in Australia (HEAR 2015), and in New Zealand, although not yet naturalized, *F. microcarpa* is recognized as a potential problem weed (HEAR 2015). In the Mediterranean region, *F. microcarpa* is mostly a weed of urban habitats (Schicchi 1999; Brandes 2007; Verloove & Reyes-Betancort 2011; Caughlin et al. 2012). In Israel, however, it is invasive but not widespread (Dufour-Dror 2013; EPPO 2015).

Invasions of *F. microcarpa* in the United States and its territories are well documented, with the exception of California. In Hawai'i, most of the main islands are infested with *F. microcarpa*, including disturbed urban sites and natural areas in wet and dry forests (Starr et al. 2003). In Florida, it is listed as a 'Category I' invasive plant, defined as alien plants that alter native plant communities by displacing species, change community structures or ecological functions, or they hybridize with natives (FLEPPC 2015). Although *F. microcarpa* has received some attention as possibly established and a potentially invasive species in California, it has not been rated or evaluated by Cal-IPC (2015).

Ficus microcarpa can propagate spontaneously from seed on many surfaces. If it is not removed, *F. microcarpa* can cause structural damage to concrete and buildings, and as an epiphyte it will eventually strangle the host tree (Weber 2003; HEAR 2015; ISSG 2015). In addition, *F. microcarpa* is a fast-growing tree that can shade out native plant species and modify competitive regimes of natural communities (Gordon 1998; ISSG 2015).

Currently, it appears that *F. microcarpa* is limited primarily to urban areas. Owing to high propagule pressure associated with widespread cultivation and the consequent large fig crop production, *F. microcarpa* will likely continue to expand its naturalized range and further invade natural areas in southern California. Native habitats most vulnerable to invasions include estuaries, floodplains and banks of tidal creeks, riparian scrub and woodlands, sloughs, and coastal bluff seeps, particularly calcareous-saline substrates. *Phoenix canariensis*, its principal host tree and an acknowledged halophyte (Menzel & Lieth 2003; Yensen 2015), is a known invader of riparian and estuary habitats in southern California (Roberts 2008; Talley et al. 2012). *Ficus microcarpa* hemi-epiphyte invasions will likely follow.

CONCLUSIONS

Mutualisms often structure ecosystems and mediate complex ecosystem functions, but they also facilitate biological invasions (Traveset & Richardson 2014). Plant species escaping cultivation must negotiate multiple biotic and abiotic barriers in order to survive, colonize, reproduce, and disperse to new sites (Richardson et al. 2000). The global movement of organisms and ornamental horticulture has promoted invasions (Mack & Lonsdale 2001; Brusati et al. 2014), sometimes by reuniting obligate plant–pollinator partnerships in new regions and environments. The *F. microcarpa–E. verticillata* mutualism represents one of the best known case studies of plant and pollinator–mediated naturalization and invasion processes, which now has also been documented for southern California.

For scientists and resource managers alike, it is logical to assume that cultivated or accidentally introduced plants with specialized pollination syndromes are unlikely to set seed. Specialized pollination makes these plants unlikely candidates for early detection management programs; they rarely find their way onto predictive invasive plant lists. Early detection and assessment are important and fundamental management objectives when dealing with invasive plant species (Rejmánek 2000). Unfortunately, early reports of new species in local floras or journals often go unnoticed by natural area managers, and voucher specimens may not be submitted to herbaria for formal documentation. Accordingly, a potentially invasive non-native species may only be recognized as troublesome decades after it was first detected (Randall 1997). Such is the case here for *F. microcarpa*. Rejmánek (2000) remarked that we should pay more attention to habitat-specific predictors, which in this scenario, should include urban environments, and microhabitats such as palm tree trunks as substrates for epiphyte invasions.

Ficus microcarpa, widely cultivated in southern California, is highly adaptable to the summer-dry Mediterranean climate. Its pollinator too, *E. verticillata*, is highly adaptive to variable syconia production in seasonal climate regimes. Once this plant–pollinator mutualism was reunited, *F. microcarpa* seeds were readily dispersed by animal vectors and germinated in microhabitats suitable for a naturally-occurring lithophyte that favors lime-rich alkaline substrates of urban structures, as well as the abundant micro-niches provided in the palm tree-rich urban landscape favored by these hemi-epiphytes. Accordingly, *F. microcarpa* is in the process of a rapid range expansion in southern California's urban environment, which will likely lead to expanded invasions of natural area habitats. Given the propensity of *Phoenix* and *Washingtonia* palms to invade estuarine and riparian ecosystems, land managers and scientists should carefully monitor these habitats for *F. microcarpa* invasive occurrences in coastal southern California.

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LITERATURE CITED

Aguirre, A., R. Guevara, M. García, and J.C. López. 2009. Fate of epiphytes on phorophytes with different architectural characteristics along the perturbation gradient of *Sabal mexicana* forests in Veracruz, Mexico. J. Veg. Sci. 21: 6–15.

Anbarashan, M. and N. Parthasarathy. 2013. Tree diversity of tropical dry evergreen forests dominated by single or mixed species on the Coromandel Coast of India. Tropical Ecology 54: 179–190.

Australian Plant Census (APC). 2015. *Ficus microcarpa* L.f. Available: https://biodiversity.org.au/nsl/services/search?product=apc&tree.id=1133571&name=ficus+microcarpa&inc._scientific=&inc.scientific=on&inc._cultivar=&inc.cultivar=on&max=100&display=apc&search=true [accessed June 2015].

Aronson, J.A. 1989. Haloph: a data base of salt tolerant plants of the world. Office of Arid Land Studies, University of Arizona, Tucson.

Baldwin, B.G., D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D.H. Wilken, eds. 2012. The Jepson manual: vascular plants of California, 2nd ed. University of California Press, Berkeley.

Basset, Y., V. Novotny, and G. Weiblen. 1997. *Ficus*: a resource for arthropods in the tropics, with particular reference to New Guinea. *in* A. Watt, N.E. Stork, and M. Hunter, eds. Forests and Insects. London: Chapman & Hall. Pp. 341–361.

Beardsley, J.W. 1998. Chalcid wasps (Hymenoptera: Chalcidoidea) associated with fruit of *Ficus microcarpa* in Hawai'i. Proc. Hawaii. Entomol. Soc. 33: 19–34.

Bell, C.E., C.A. Wilen, and A.E. Stanton. 2003. Invasive plants of horticultural origin. HortScience 38: 14–16.

Berg, C.C. 2003. Flora Malesiana precursor for the treatment of Moraceae 1. The main subdivision of *Ficus*: the subgenera. Blumea 48: 167–178.

Berg, C.C. 2004. Flora Malesiana precursor for the treatment of Moraceae 7: *Ficus* subgenus *Urostigma*. Blumea 49: 463–480.

Berg, C.C. and E.J.H. Corner. 2005. Moraceae-*Ficus*. Flora Malesiana Series I (Seed Plants) 17: 1–730.

Bossard, C.C., R.P. Randall, and M.C. Horshovsky. 2000. Invasive plants of California's wildlands. University of California Press, Berkeley, Los Angeles.

Brandes, D. 2007. Epiphytes on *Phoenix canariensis* in Dalmatia (Croatia). Available: http://www.digibib.tu-bs.de/?docid=00018886 [accessed Sept 2015].

Brenzel, K.N., ed. 2007. Western garden book, 8th ed. Sunset Books, Sunset Publishing Corporation, Menlo Park, CA.

Brownsey, J.P. and C.N. Page. 1986. Tree-fern skirts: a defense against climbers and large epiphytes. J. Eco. 74: 787–796.

Brusati, E.D., D.W. Johnson, and J.M. DiTomaso. 2014. Predicting invasive plants in California. Calif. Agric. 68: 89–95.

Burrows, J. and S. Burrows. 2003. Figs of Southern & South-Central Africa. Umdaus Press, Hatfield, South Africa.

California Department of Food and Agriculture (CDFA). 1994. California plant pest and disease report. R.J. Gill, ed. Vol. 13, Numbers 3-4, July-September 1994, Sacramento, CA.

California Native Plant Society (CNPS). 2007. Los Angeles/Santa Monica Mountains Chapter, January-February 2007. Toyon 27: 7.

Cal-IPC. 2015. California Invasive Plant Council. Available: http://www.cal-ipc.org/ [accessed July 2015].

Caughlin, T., J.H. Wheeler, J. Jankowski, and J.W. Lichstein. 2012. Urbanized landscapes favored by fig-eating birds increase invasive but not native juvenile strangler fig abundance. Ecology 93: 1571–1580.

Chaudhary, L.B., J.V. Sudhakar, A. Kumar, O. Bajpai, R. Tiwari, and G.V.S. Murthy. 2012. Synopsis of the genus *Ficus* L. (Moraceae) in India. Taiwania 57: 193–216.

Chew, W.L. 1989. Moraceae. *in* Flora of Australia, Vol. 3. Australian Government Publishing Service, Canberra. Pp. 15–68.

City of Santa Monica (CSM). 2015. Santa Monica urban forest, Los Angeles County, California. Available: http://www.smgov.net/Portals/UrbanForest/content.aspx?id=14794 [accessed October 2015].

Clarke, O.F., D. Svehla, G. Ballmer, and A. Montalvo. 2007. Flora of the Santa Ana River and environs. Heyday Books, Berkeley, CA.

Compton, S.G. and M.K. Musgrave. 1993. Host relationships of *Ficus burtt-davyi* when growing as a strangler fig. S. Afr. J. Bot. 59: 425–430.

Consortium of California Herbaria (CCH). 2015. *Ficus microcarpa*. Available: http://ucjeps.berkeley.edu/consortium/ [accessed Jan–Apr 2015].

Cook, J.M. and J.Y. Rsaplus. 2003. Mutualists with attitude: coevolving fig wasps and figs. TREE 18: 241–248.

Corlett, R.T. 2006. Figs (*Ficus*, Moraceae) in urban Hong Kong, South China. Biotropica 38: 116–121.

Corner, E.J.H. 1997. Wayside trees of Malaya, 4th ed. Malayan Nature Society, Kuala Lumpur. Vol. 1: 1-476/Vol. 2: 477–861.

Crooks, K.R., A.V. Suarez, and D.T. Bolger. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biol. Cons. 115: 451–462.

Cruaud, A., J.Z. Roula, G. Genson, C. Cruaud, A. Couloux, F. Kjellberg, S. van Noort, and J.Y. Rasplus. 2010. Laying the foundations for a new classification of Agaonidae (Hymenoptera: Chalcidoidea), a multilocus phylogenetic approach. Cladistics 26: 359–387.

Dean, E., F. Hrusa, G. Leppig, A. Sanders, and B. Ertter. 2008. Catalogue of nonnative vascular plants occurring spontaneously in California beyond those addressed in The Jepson Manual–Part II. Madroño 55: 93–112.

Dehgan, B. 1998. Landscape plants for subtropical climates. University Press of Florida, Gainesville.

DeNiro, M.J., E.M. Lord, L.S. Sternberg, and I.P. Ting. 1985. Crassulacean Acid Metabolsim in the strangler *Clusia rosea* Jacq. Science 229: 969–971.

DiTomaso, J.M., and E.A. Healy. 2003. Aquatic and riparian weeds of the West. U.C. Agriculture and Natural Resources Publication 3421, Oakland, CA.

DiTomaso, J.M. and E.A. Healy. 2007. Weeds of California and other western states, Vol. 2, Geraniaceae–Zygophyllaceae. U.C. Agriculture and Natural Resources Publication 3488, Oakland, CA.

Doty, W.L. and P.C. Johnson, eds. 1954. Western garden book. Sunset Magazine, Lane Publishing Company, Menlo Park, CA.

Dufour-Dror, J.M., ed. 2013. Israel's least wanted alien ornamental plant species. Ministry of Environmental Protection, Ministry of Agriculture, Nature & Parks Authority, and Hebrew University Botanical Gardens, Israel.

European and Mediterranean Plant Protection Organization (EPPO). 2015. Global Database: invasive alien plants in Israel. Available: https://gd.eppo.int/reporting/article-2506 [accessed November 2015].

Flora of North America (FNA). 2015. Taxonomic treatments for families and species. Available: http://www.efloras.org/flora_page.aspx?flora_id=1 [accessed July-December 2015].

Florida Exotic Pest Plant Council (FLEPPC). 2015. List of invasive plant species. Available: http://www.fleppc.org/list/list.htm [accessed May 2015].

Gardner, R.O. and J.W. Early. 1996. The naturalization of banyan figs (*Ficus* spp., Moraceae) and their pollinating wasps (Hymenoptera: Agaonidae) in New Zealand. New Zealand J. Bot. 34:103–110.

Garrett, K. L. 1997. Population status and distribution of naturalized parrots in southern California. Western Birds 28: 181–195.

Garrett, K.L. 1998. Population trends and ecological attributes of introduced parrots, doves and finches in California. Paper 49, Proceedings of the Eighteenth Vertebrate Pest Conference (1998).

Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Eco. Appl. 8: 975–989.

Government of Bermuda (GB). 2015. Invasive species: Indian laurel, *Ficus microcarpa*. Department of Conservation Services, Ministry of Health, Seniors and Environment. Available: http://www.conservation.bm/indian-laurel [accessed July 2015].

Grewell, B.J., J.C. Callaway, and W.R. Ferren, Jr. 2007. Estuarine wetlands. *in* M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, eds. Terrestrial vegetation of California, ed. 3. University of California Press, Berkeley, Los Angeles, London. Pp. 124–154.

Harrison, R.D. 2005. Figs and the diversity of tropical rainforests. BioScience 55: 1053–1064.

Hatch, C.R. 2007. Trees of the California landscape. University of California Press, Berkeley, Los Angeles, London.

Hawaiian Ecosystems at Risk Project (HEAR). 2015. *Ficus microcarpa*. http://www.hear.org/species/ficus_microcarpa/ [accessed July 2015].

Herre, E.A., C.A. Machado, E. Bermingham, J.D. Nason, D.M. Windsor, S.S. McCafferty, W. Van Houten, and K. Bachmann. 1996. Molecular phylogenies of figs and their pollinator wasps. J. Biogeogr. 23: 521–30.

Hodel, D.R. 2014. *Washingtonia* × *filibusta* (Arecaceae: Coryphoideae), a new hybrid from cultivation. Phytoneuron 2014-68: 1–7.

Hrusa, F., B. Ertter, A. Sanders, G. Leppig, and E. Dean. 2002. Catalogue of non-native vascular plants occurring spontaneously in California beyond those addressed in The Jepson Manual–Part I. Madroño 46: 61–98.

Invasive Species Specialist Group (ISSG). 2015. Global Invasive Species Database: *Ficus microcarpa*. Available: www.issg.org [accessed May 2015].

Janzen, D.H. 1979. How to be a fig. Annu. Rev. Ecol. Syst. 10: 13–51.

Jepson Flora Project. 2015 (v. 1.0 with Supplements). Jepson eFlora, *Ficus microcarpa*. Available: http://ucjeps.berkeley.edu/IJM.html [accessed April 2015].

Jim, C.Y. 1998. Old stone walls as an ecological habitat for urban trees in Hong Kong. Lands. Urban Plan. 42: 29-43.

Jim. C.Y. and W.Y. Chen. 2011. Bioreceptivity of buildings for spontaneous arboreal flora in compact city environment. Urban For. Urban Greening 10: 19–28.

Kaufman, S.R. and W. Kaufman. 2012. Invasive plants: a guide to identification, impacts, and control of common North American species, 2nd ed. Stackpole Books, Mechanicsburg, PA.

Kaufmann, S., D. Mckey, M. Gossaert-Mckey, and C.C. Horvitz. 1991. Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). Am. J. Bot. 78: 971–977.

Keng, H., S.C. Chin, and H.T.W. Tan. 1990. The concise flora of Singapore: Gymnosperms and Dicotyledons. Singapore University Press, Singapore.

Kramer, G. 2011. Palm tree susceptibility to hemi-epiphytic parasitism by *Ficus*. Master of Science Thesis, University of Florida, Gainesville.

Krishen, P. 2006. Trees of Delhi: a field guide. Dorling Kindersley, Delhi, India.

Laman, T.G. 1995. *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. Ecology 76: 2617–2626.

Li, H.E., B.T. Li, and S.F. Lan. 2005. Responses of the urban roadside trees to traffic environment. Acta Ecol. Sin. 25: 2180–2187.

Lok, A.F., W.F. Ang, B.Y.Q. Ng, T.M. Leong, C.K. Yeo, and H.T.W. Tan. 2013. Native fig species as a keystone resource for the Singapore urban environment. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

Machado, C.A., N. Robbins, M.T.P. Gilbert, and E.A. Herre. 2005. Critical review of host specificity and its coevolutionary implications in the fig fig-wasp mutualism. Proc. Natl. Acad. Sci. U.S.A. 102: 6558–6565.

Mack, R.N. and M. Erneberg. 2002. The United States naturalized flora: largely the product of deliberate introductions. Ann. Mo. Bot. Gard. 89: 176–189.

Mack, R.N. and W.M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. BioScience 51: 95–102.

Male, T.D. and G.E. Roberts. 2005. Host associations of the strangler fig, *Ficus watkinsiana,* in a subtropical Queensland rain forest. Aust. Ecol. 30: 229–236.

McKey, D. 1989. Population biology of figs: applications for conservation. Experientia 45: 661–673.

McMinn, H.E. and E. Maino. 1981. An illustrated manual of Pacific Coast trees. University of California Press, Berkeley, Los Angeles, London.

McPherson, J.R. 1999. Studies in urban ecology: strangler figs in the urban parklands of Brisbane, Queensland, Australia. Aust. Geogr. Stud. 37: 214–229.

McPherson, E.G., J.R. Simpson, P.J. Peper, and Q. Xiao. 2001. Benefit-cost analysis of Santa Monica's municipal forest. Center for Urban Forest Research, USDA Forest Service, Pacific Southwest Research Station, and Department of Land, Air, and Water Resources, University of California, Davis, CA.

Menzel, U. and H. Lieth. 2003. Halophyte database version 2.0. *in* H. Lieth and M. Mochtchenko, eds. Cash crop halophytes: recent studies. Kluwer Academic Publishers, Dordrecht. Pp. 221–250.

Nadel, H., J.H. Frank, and R.J. Knight, Jr. 1992. Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. Fla. Entomol. 75: 29–38.

Nowak, D.J., R.E. Hoehn III, D.E. Crane, L. Weller, and A. Davila. 2011. Assessing urban forest effects and values, Los Angeles' urban forest. U.S. Department of Agriculture, Forest Service, Northern Resource Bulletin NRS-47, Newtown Square, PA.

O'Brien, M. 1995. A new invasive? CalEPPC News 3: 5.

Pemberton, C.E. 1939. Note on introduction and liberation of *Eupristina verticillata* Waterston in Honolulu. Proc. Hawaii. Entomol. Soc. 10: 182.

Perry, R. 2010. Landscape plants for California gardens. Land Design Publishing, Pomona, CA.

Porcher, M.H. 2015. Sorting *Ficus* names. Multilingual multiscript plant name database–a work in progress, 1995–2020. University of Melbourne. Australia. Available: http://www.plantnames.unimelb.edu.au/Sorting/Ficus.html > [accessed October 2015].

Prigge, B.A. and A.C. Gibson. 2012. A naturalist's flora of the Santa Monica Mountains and Simi Hills, California. Web version, included in Wildflowers of the SMMNRA. Available: http://www.smmflowers.org/bloom/UCLA_PDFs_Web.htm [accessed July 2015].

Putz, F.E. and N.M. Holbrook. 1989. Strangler fig rooting habits and nutrient relations in the Llanos of

Venezuela. Am. J. Bot. 76: 781–788.
Ramírez, W.B. and J.S. Montero. 1988. *Ficus microcarpa* L., *F. benjamina* L. and other species introduced in the New World, their pollinators (Agaonidae) and other fig wasps. Rev. Biol. Trop. 36: 441–446.
Randall, J.M. 1997. Weed alert! New invasive weeds in California. *in* M. Kelly, E. Wagner, and P. Warner, eds. Symposium Proceedings of the California Exotic Plant Pest Council, 1997, Vol. 3: 19–24.
Randall, R.P. 2012. A global compendium of weeds, 2nd ed. Department of Agriculture and Food, Western Australia.
Rauch, F. and P. Weissich. 2000. Plants for tropical landscapes. University of Hawai'i Press, Honolulu.
Rebman, J.P. and M.G. Simpson. 2006. Checklist of the vascular plants of San Diego County, 4th ed. San Diego Natural History Museum, San Diego, CA.
Reichard, S.H. and P. White. 2001. Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51: 103–113.
Rejmánek, M. 2000. Invasive plants: approaches and predictions. Aust. Ecol. 25: 497–506.
Richardson, D.M., N. Allsopp, C.M. D'Antonio, S.J. Milton, and M. Rejmánek. 2000. Plant invasions: the role of mutualism. Biol. Rev. 75: 65–93.
Ridley, H.N. 1924. The Flora of the Malay Peninsula. Vol. III–Apetalae (1967 Reprint). A. Asher & Co., Amsterdam, and L. Reeve & Co., Brook N. Ashford, Great Britain.
Riefner, R.E., Jr. and A.R. Smith. 2015. *Nephrolepis cordifolia* (Nephrolepidaceae) naturalized in southern California (U.S.A.): with notes on unintended consequences of escaped garden plants. J. Bot. Res. Inst. Texas 9: 201–212.
Roberts, F.M., Jr. 2008. The vascular plants of Orange County, California: an annotated checklist. F.M. Roberts Publications, Encinitas, CA.
Roberts, F.M., Jr., S.D. White, A.C. Sanders, D.E. Bramlet, and S. Boyd. 2004. The vascular plants of western Riverside County, California: an annotated checklist. F.M. Roberts Publications, San Luis Rey, CA.
Rønsted, N., G.D. Weiblenb, V. Savolainena, and J.M. Cook. 2008. Phylogeny, biogeography, and ecology of *Ficus* section Malvanthera (Moraceae). Mol. Phylogent. Evol. 48: 12–22.
Schicchi, R. 1999. Spontaneizzazione di *Ficus microcarpa* L. (Moraceae) e *Cardiospermum grandiflorum* Sw. (Sapindaceae) in Sicilia. Naturalista Siciliano 23: 315–317.
Schmidt, S. and D.P. Tracey. 2006. Adaptations of strangler figs to life in the rainforest canopy. Functi. Plant Biol. 33: 465–475.
Shanahan M, S. So, S.G. Compton, and R. Corlett. 2001. Fig-eating by vertebrate frugivores: a global review. Bio. Rev. 76: 529–572.
Shuyi, C. 2009. Threat and weediness attributes of *Ficus* (Moraceae). Bachelor of Science Thesis, National University of Singapore, Singapore.
Simono, S. 2012. *Washingtonia*. *in* B.G. Baldwin, D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D.H. Wilken, eds. The Jepson manual: vascular plants of California, 2nd ed. University of California Press, Berkeley. P. 1303.
Stange, L.A. and R.J. Knight, Jr. 1987. Fig pollinating wasps of Florida (Hymenoptera: Agaonidae). Vol. 296, Entomology Circular, Division of Primary Industry, Florida Department of Agriculture and Consumer Service, FL.
Starr, F., K. Starr, and L. Loope. 2003. *Ficus microcarpa*. United States Geological Survey, Biological Resources Division, Haleakala Field Station, Maui, Hawai'i.
Tan, H.T.W., C. K. Yeo, and A.B.C. Ng. 2009. Native and naturalized biodiversity for Singapore waterways and water bodies No. 1. *Ficus microcarpa*, Malayan Banyan. Raffles Museum of Biodiversity Research, National University of Singapore, and Singapore-Delft Water Alliance, Faculty of Engineering, National University of Singapore, Singapore. Available: http://rmbr.nus.edu.sg/raffles_museum_pub/ficus_microcarpa.pdf [accessed Mar 2015].

Talley, T.S., K.C. Nguyen, and A. Nguyen. 2012. Testing the effects of an introduced palm on a riparian invertebrate community in southern California. PLoS One. Available: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3411789/ [accessed October 2015].

The Plant List. 2015. *Ficus microcapra* L.f./*Ficus retusa* L. Available: http://www.theplantlist.org/browse/A/Moraceae/Ficus/ [accessed June 2015].

Todzia, C. 1986. Growth habits, host tree species, and density of hemiepiphytes on Barro Colorado Island, Panama. Biotropica 18: 22–27.

Traveset, A. and D.M. Richardson. 2014. Mutualistic interactions and biological invasions. Annu. Rev. Ecol. Evol. Syst. 45: 89–113.

Trent, H. and J. Seymour. 2010. Examining California's first palm tree: the Serra palm. J. San Diego Hist. 56: 105–120.

United States Department of Agriculture, Agricultural Research Service, Germplasm Resources Information Network (USDA, GRIN). 2015. *Ficus microcarpa* L.f.. National Germplasm Resources Laboratory, Beltsville, MD. Available: http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?16897 [accessed Apr 2015].

United States Department of Agriculture, Natural Resource Conservation Service (USDA, NRCS). 2015. *Ficus microcarpa*. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. Available: http://plants.usda.gov/core/profile?symbol=FIMI2 [accessed Apr–Nov 2015].

Uotila, P. 2011. *Ficus microcarpa*, Moraceae. *in* Euro+Med Plantbase-the information resource for Euro-Mediterranean plant diversity. Available: http://ww2.bgbm.org/EuroPlusMed/PTaxonDetailOccurrence.asp?NameId=7720877&PTRefFk=7300000 [accessed August 2015].

van Ham, C., P. Genovesi, and R. Scalera. 2013. Invasive alien species: the urban dimension. IUCN European Union Representative Office, Brussels, Belgium.

van Noort, S. and J.Y. Rasplus. 2015. Figweb: figs and fig wasps checklist of Indo-Australasian *Ficus* (Moraceae). Available: http://www.figweb.org/Ficus/Checklists/Checklist_Indo-Australasian_Ficus.htm [accessed March 2015].

Verloove, F. and J. A. Reyes-Betancort. 2011. Additions to the flora of Tenerife (Canary Islands, Spain). Coll. Bot. 30: 63–78.

Wagner, K., G. Mendieta-Leiva, and G. Zotz. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. AoB PLANTS 7: plu092; doi:10.1093/aobpla/plu092.

Wagner, W.L., D.R. Herbst, and S.H. Sohmer. 1999. Manual of the flowering plants of Hawai'i. Bishop Museum Special Publication 83, University of Hawai'i and Bishop Museum Press, Honolulu.

Wang, R. 2014. The fig wasps associated with *Ficus microcarpa*, an invasive fig tree. PhD Thesis, University of Leeds, Leeds, UK.

Wang, R., R. Aylwin, L. Barwell, and 20 others. 2015. The fig wasp followers and colonists of a widely introduced fig tree, *Ficus microcarpa*. Insect Conservation and Diversity, The Royal Entomological Society. Available: http://onlinelibrary.wiley.com/doi/10.1111/icad.12111/abstract [accessed April 2015].

Weber, E. 2003. Invasive plant species of the world: a reference guide to environmental weeds. CABI Publishing, Wallingford, U.K.

Weiblen, G.D. 2002. How to be a fig wasp. Ann. Rev. Entomol. 47: 299–330.

Wen, D., Y. Kuang, and G. Zhou. 2004. Sensitivity analyses of woody species exposed to air pollution based on ecophysiological measurements. Environ. Sci. Polluti. R. 11: 165–170.

Whittemore, A.T. and E. McClintock. 2012. *Ficus*. *in* B.G. Baldwin, D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D.H. Wilken, eds. The Jepson manual: vascular plants of California, 2nd ed. University of California Press, Berkeley. Pp. 910–911.

Wikipedia. 2015. Portland cement. Available: https://en.wikipedia.org/wiki/Portland_cement [accessed July 2015].

Wunderlin, R.P. 1997. *Ficus* (Moraceae). *in* Flora of North America Editorial Committee, eds. Flora of North America north of Mexico, Vol. 3, Pteridophytes and Gymnosperms. Oxford University Press, New York, New York. Pp. 388–389.

Yang, H.W., H.Y. Tzeng, and L.S. Chou. 2013. Phenology and pollinating wasp dynamics of *Ficus microcarpa* L.f.: adaptation to seasonality. Bot. Stud. 54: 11. Available: http://www.as-botanicalstudies.com/content/pdf/1999-3110-54-11.pdf [accessed October 2015].

Yensen, N.P. 2015. Halophyte database: salt-tolerant plants and their uses. USDA-ARS, U.S. Salinity Laboratory, Riverside, CA. Available: http://www.ussl.ars.usda.gov/pls/caliche/halophyte.query [accessed Apr 2015].

Yeo, C.K. and H.T.W. Tan. 2011. *Ficus* stranglers and *Melastoma malabathricum*: potential tropical woody plants for phytoremediation of metals in wetlands. Nature in Singapore 4: 213–226.

Zona, S. 2008. The horticultural history of the Canary Island date palm (*Phoenix canariensis*). Garden History 36: 301–309.

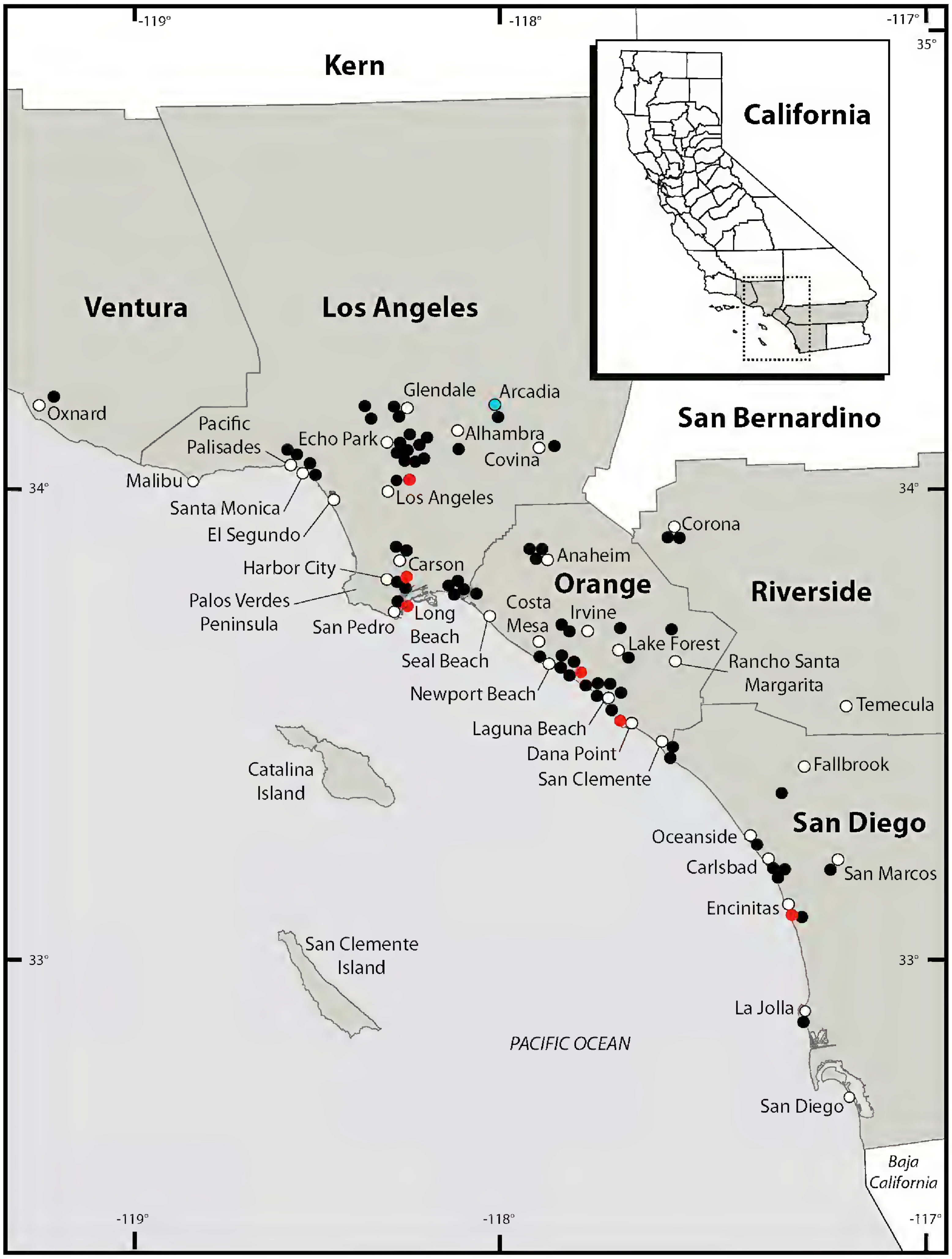

Figure 1. Known naturalized distribution of *F. microcarpa* in southern California: a solid circle (●) depicts locations documented in urban and native habitats; a red circle (●) identifies the largest of the naturalized trees observed during this study; and a blue circle (●) identifies the approximate location (Arcadia) of the first documented record of its pollinating fig wasp, *E. verticillata*, for California.

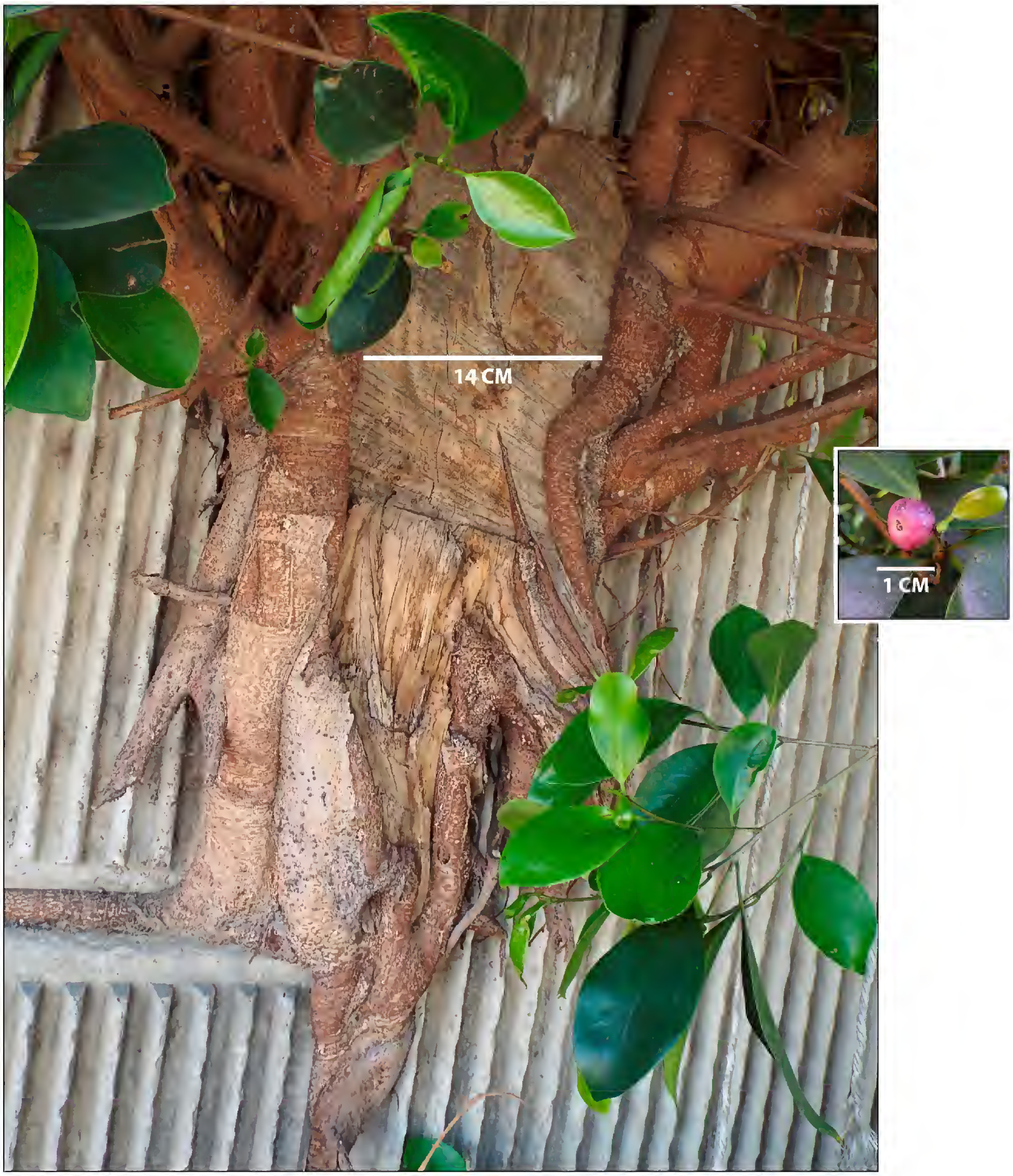

Figure 2. View of an approximately 5 m tall *F. microcarpa* tree growing on rough-grouted concrete wall at Harbor City, Los Angeles County. Note aerial and adventitious roots and tree base that has been cut back during landscape maintenance activities. Inset photograph showing mature syconium.

Figure 3. Approximately 3.5 m tall *F. microcarpa* tree growing from the side of a concrete reinforced bulkhead along harbor shores at San Pedro, Los Angeles County. Inset photograph showing mature and developing syconia. The Los Angeles Maritime Museum is in the background.

Figure 4. View of an approximately 3.2 m tall *F. microcarpa* tree rooted in an expansion joint of the 43rd Street bridge on the 110 Freeway, City of Los Angeles. Note water stains on bridge and retaining wall from urban runoff, and cultivated *F. microcarpa* tree planted along Flower St. the in upper right-hand side of photograph. Inset photograph showing immature syconia.

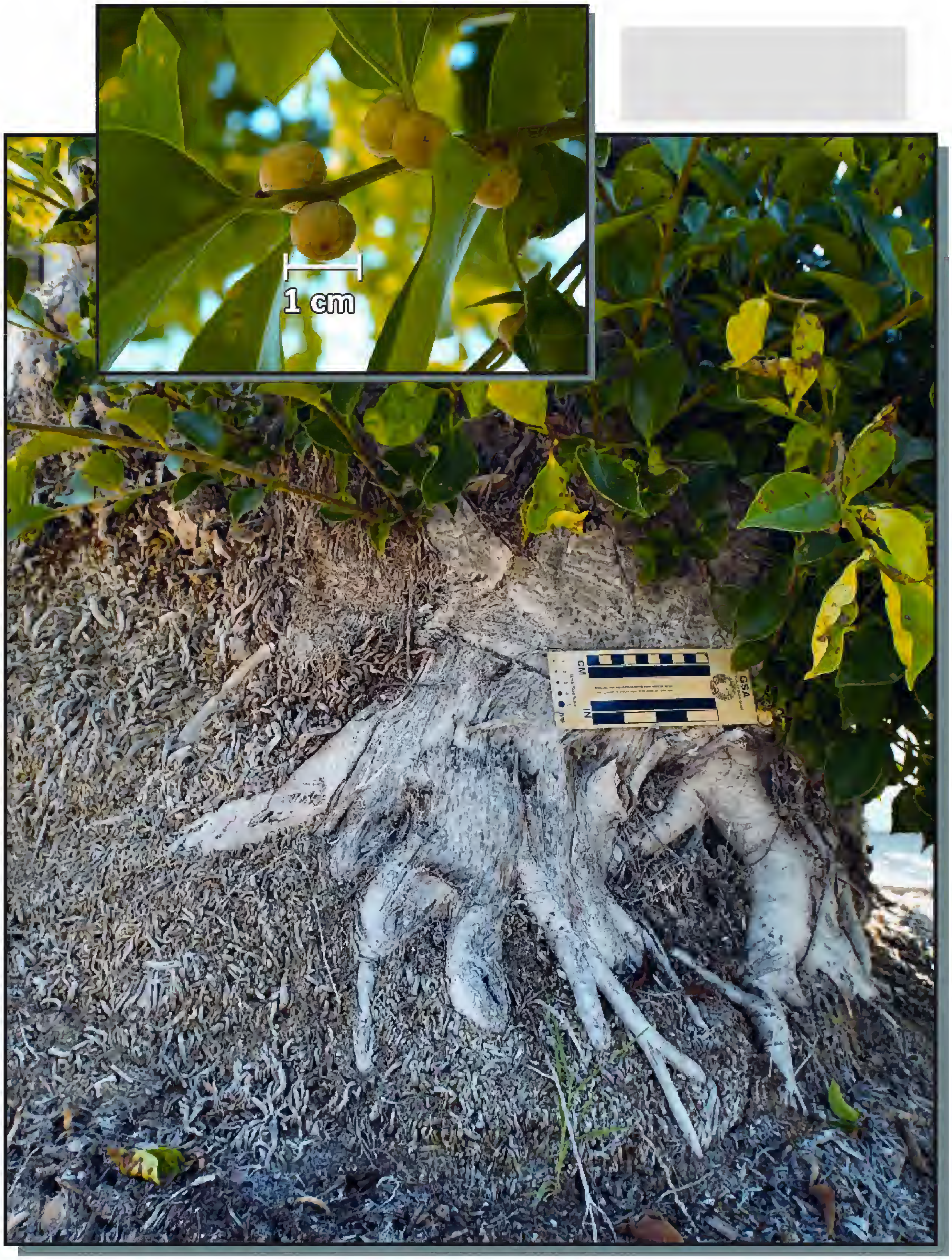

Figure 5. View of an approximately 3 m tall *F. microcarpa* tree growing on the base of a cultivated *P. canariensis* palm tree in Newport Beach, Orange County. Note the base (ca. 28 cm wide) of *F. microcarpa* has been cut back during landscape maintenance activities. Inset photograph showing immature syconia.

Figure 6. View of an approximately 3 m tall *F. microcarpa* tree growing at the base of a calcareous-saline sandstone cliff in Dana Point, Orange County. Many *Ficus* species that are hemi-epiphytes are also lithophytes, thereby enabling colonization of many urban and native habitats in southern California. Inset photograph shows immature syconia.

Figure 7. *Ficus microcarpa* growing on the trunk of *P. canariensis* cultivated in Encinitas, San Diego County. Note *F. rubiginosa* growing on the upper trunk.

Figure 8. View of *F. microcarpa* growing at the base of *Washingtonia robusta* in Oceanside, San Diego County. This was the smallest fertile plant observed during the study.

Figure 9. *Ficus microcarpa* grows in joints of old masonry and crumbling brick walls, Laguna Beach, Orange County. Note the base has been cut back during landscape maintenance activities.

Figure 10. View of *F. microcarpa* juvenile plant growing on the trunk of *P. canariensis*, Corona City Park, western Riverside County. Plants at the inland extremes of its current range may be influenced by aerosol drift from urban irrigation spray heads.

Figure 11. *Ficus microcarpa* grows in calcareous-saline soils on the bank of a tidal urban channel, Dominquez Channel, Carson, Los Angeles County. Perennial forbs in the photograph are *Parietaria judaica* L. (Urticaceae), another urban weed occasionally found in coastal native habitats.

Figure 12. *Ficus microcarpa* occurs rarely in native plant communities along the immediate coast. This approximately 1 m tall shrub grows on a calcareous-saline outcrop in Laguna Beach, Orange County. Note ephemeral seepage and salt crust formation on the outcrop surface.

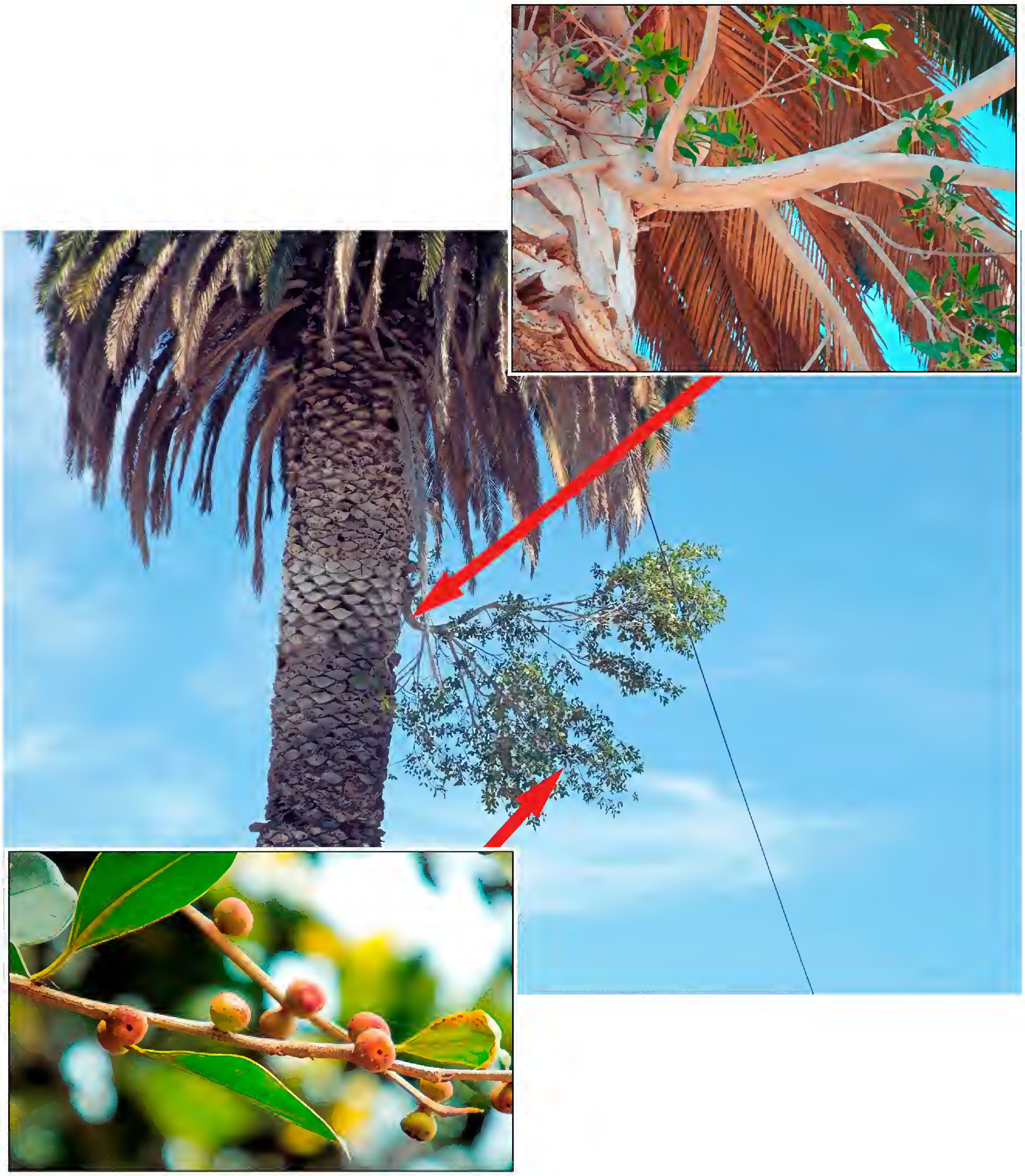

Figure 13. *Ficus microcarpa* (*Riefner 15-135 photographic voucher*) grows on the upper trunks of palm trees, mostly *P. canariensis,* at inland and coastal localities. Moist coastal breezes, ocean fogs, and perhaps the inland extent of the marine layer, likely provide moisture to aid seedling establishment and persistent growth of *F. microcarpa* hemi-epiphytes growing in arid southern California. Inset photographs depict point of basal attachment and immature syconia. Photographs were taken in Carlsbad, San Diego County.

Figure 14. *Ficus microcarpa*, a strangler fig, is epiphytic on a palm tree trunk with *Nephrolepis cordifolia* in Long Beach, California. Note persistent leaf bases of *Butia capitata*. Inset photograph shows root basket formation typical of strangler figs that constrict and gradually kill host trees.